20 Genetic Resources and Conservation of Mahogany in Mesoamerica

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Abstract: We review here the scale of neutral and adaptive genetic variation of mahogany (*Swietenia* spp.), one of the most valuable tree species in the world, and relate this information directly to provenance performance, and seed transfer and sourcing recommendations. Further, we explore a series of scientific issues directly related to critical day-to-day management of mahogany, giving guidelines to maximise genetic diversity outcomes in natural, remnant, sustainably harvested, and/or restored forest landscapes. The study concludes that conservation and sustainable management of mahogany genetic resources cannot be simply defined in terms of one-size-fits-all solutions, and requires local community involvement to prevent illegal logging and ensure mutual benefit. Landscape level strategies for the effective management of mahogany trees outside of forests urgently need to be developed, together with strategies to promote the benefits of different agroforestry practices. There is also a requirement for conservation planners to consider that trees found outside protected areas have a role in the conservation. In wide-ranging species, promoting international collaboration for collecting, characterising, and conserving genetic resources is vital as international consensus is needed to streamline phytosanitary procedures, to facilitate the exchange of forest reproductive material, and assist genetic resource conservation efforts.

Keywords: mahogany, *Swietenia*, conservation, management, policies, genetic diversity, genetic resource, agroforestry

20.1 Introduction

Mahogany is one of the most highly valued timbers in the world. It has been economically vital for isolated communities in many countries in Mesoamerica; in counterpart, exploitation of mahogany in South American countries has been developed by enterprises with higher economic capacity. Within its natural range, some deprived communities still depend exclusively on the use of this species as a raw material for making handicrafts and valuable furniture, including doors, tables, and desks. However, the species is also used broadly in international markets to produce a diverse range of products, for example, building yachts and other luxury goods. Mahogany is the most important native species in terms of the volume exported from Guatemala, with more than 80% of the total volume (CONAP 2008). Much of this wood is logged by community concessions that are of highly socioeconomic importance for livelihoods in areas where there are no other income options. In other countries, the exploitation is made by companies and the income is not perceived by the communities.

The prices of mahogany wood are among the highest timber prices in the world; currently, the price is around USD 1700 (Ortiz 2007). W could not get recent information or publications on the exports and imports, but we did get access to the database of the Convention on International Trade in Endangered Species (CITES), from which we summarised the exports and imports for all the countries. From 2006 to 2009, the exports were around 113 510 cubic meters, and the imports for the same years were 111 602

cubic meters (UNEP-WCMC 2010). Data on the internal use of mahogany at the country level was also not accessible.

In general, a decrease in mahogany exports since 2002 has occurred in the main exporting countries, but another species, *Cedrela odorata* (Spanish-cedar, a member of the mahogany family, Meliaceae), has been logged for export and is called the "new mahogany." In 2008, an internal report by National Institute for Natural Resources (INRENA) estimated that as much as 70% of the *Cedrela odorata* exports could have been of illegal origin (INRENA 2008).

Logging of mahogany is frequently correlated with increased deforestation rates, as ranchers and smallholder agriculturalists follow logging roads into previously inaccessible frontier regions (Veríssimo et al.1995). In this case study, we consider the issues of genetic diversity, mating systems, seed- and timber-sourcing, and genetic resource management and relate them to strategies for the conservation, sustainable use, and restoration of mahogany populations. Complementary reviews on demography have been made by Grogan et al (2008).

Genetic diversity is the basis for adaptability and is essential for long term stability of populations and tree breeding for production, whether in plantations or by natural regeneration. It provides the potential for species to resist pests and diseases, and adapt to different environments. The conservation of genetic diversity and genetic resources is particularly recognised by the Intergovernmental Panel on Climate Change (IPCC 2007) as important for adaptation to predicted climate change. Deforestation reduces the genetic diversity of trees through direct loss of diversity, disruption of gene flow, and genetic isolation (Lowe et al. 2005), which can lead to inbreeding and associated reductions in fitness (Bawa and Dayanandan 1998). But within certain limits, gene flow and resilience allows forest trees to adapt to fragmentation.(Hamrick 2004). Added to these impacts, economically important species are faced with additional pressures, such as selective removal of phenotypically superior individuals during logging (possible dysgenic selection) and consequent devaluation of the remaining stand (Navarro and Hernandez 2004, Cornelius et al. 2005).

The contrasting interests of production and ecological restoration mirror underlying scientific issues. The source of planting stock needs to be considered at both the population level and the individual level; i.e., which populations and which trees within that population? The key scientific question is how gene flow and selection interact to influence population delimitation and reproductive fitness. The relationship between genetic diversity, habitat heterogeneity, and the scale of adaptation in trees is complex and involves a variety of factors. Gene flow may counteract even fairly strong selection and prevent the formation of locally adapted populations, although very strong environmental variation (hence selection pressure) may produce adaptive differences over short distances, despite continued high levels of gene flow (Broadhurst et al. 2008). Since the genetic composition of seed is affected by patterns of pollen flow, the extent of localised adaptation and fitness may vary with pollen flow from differing environments.

Human disturbance can thus have considerable and far-reaching genetic consequences through its impact on changing patterns of pollen flow (Lowe et al. 2005). Furthermore, deforestation and other environmental changes may mean that previously well-adapted local populations become less so. In this context, the dangers of using inbred germplasm in tree species are clear. Trees generally carry high genetic loads (deleterious recessive alleles, see Williams and Savolainen 1996) such that inbreeding and, in particular selfing, may lead to reduced fertility, slower growth in progeny, and increased susceptibility to pests or diseases (e.g., Park and Fowler 1982, Sim 1984, Griffin 1991). Furthermore, deforestation and other environmental changes may reduce the adaptive potential of local populations, a dangerous scenario when coupled with altered patterns of pollen flow and reductions in genetic diversity.

This chapter uses mahogany (*Swietenia* spp.) as a case study to show how policy and management issues can be directly addressed through studies of the levels and scales of adaptive/neutral genetic variation and gene flow across fragmented landscapes. The chapter examines a series of scientific issues that are directly related to critical day-to-day management and policy drivers that aim to maximise biodiversity outcomes (predominantly genetic diversity) in natural, remnant, sustainably harvested, and/or restored forest landscapes.

In particular, we examine:

1. The level and scale of adaptive/neutral genetic variation – related directly to provenance delineation, seed transfer guidelines, and what should be understood when people talk about using a local "seed source."
2. Genetic dynamics and mating patterns in mahogany – related directly to good seed collection practice.
3. Lessons for managing natural forests and landscape contexts.
   - Sustainable logging – How many seed trees to leave?
   - Potential for tracing timber source
   - Harnessing natural regeneration and directing forest restoration
   - Fragmentation and trees outside of forests
   - Biodiversity corridors and landscape mosaics

We will also identify opportunities and threats for the conservation and sustainable use of mahogany genetic resources, and the best examples of institutional capacities.

Swietenia species, extraction history and ecology

The genus *Swietenia* comprises three species, all of which are restricted to the neotropics and with geographical distributions that are almost completely separate.

- *Swietenia humilis* – Pacific Coast Mahogany. Pacific watershed of Central America/Mexico.
- *Swietenia macrophylla* – Big Leaf Mahogany. Atlantic watershed of Central America/Mexico, in South America south to Bolivia.
- *Swietenia mahagoni* – West Indian Mahogany. Southern Florida, Cuba, Jamaica, Hispaniola.

Swietenia spp. (mahogany) has a long history of being logged. More recently, commercial exploitation has intensified as improved logging techniques and expanding transportation networks have made it possible to cut timber at ever greater distances from markets. Cutting moves from population to population as sources become commercially viable. Changes in land use have also had severe effects on mahogany populations. Increasing use of land for agriculture, cattle farming, urbanisation, and forest exploitation has increased habitat fragmentation. The distribution and demographic density of mahogany has consequently declined markedly. For example, in Central America, the presence of natural forests that contain important populations of mahogany has been reduced to one-third of that originally surveyed by Lamb (1966), see maps in Navarro et al. (2003). Depletion of *Swietenia* spp. requires action to conserve its genetic resources in order to ensure the adaptive potential of natural populations, as well as to provide material for selection for restoration and plantation. All three *Swietenia* species are currently listed on CITES Appendix II, which restricts their international trade to legally sourced and sustainably managed supplies.

Swietenia species are early- to mid-succession, long-lived trees that reach or surpass the canopy of mature forest, requiring moderate to high light for successful establishment and good early growth. Regeneration after logging is the main issue for sustaining natural forest populations. Key factors include adequate seed sources and germination, and appropriate sites and light conditions for establishment. Complete removal of populations poses a threat, as do population reductions from logging or forest fragmentation, which may reduce genetic variation and lead to increased isolation and inbreeding. Equally, however, "sustainable" logging strategies may fail to maintain populations if gap creation is inadequate to provide appropriate light conditions to allow regeneration (Grogan et al. 2008). Both conservation and effective management are required for maintenance of genetic resources.

20.2 Regional Genetic Variation and Provenancing

Considerations of sustainability, ecological restoration, and conservation of biodiversity often lead to promotion of "local" seed sources for planting. However, the concept of "local" is a relative one, depending on the scale over which adaptation occurs. The definition of "local" seed collection zones is often arbitrary in the absence of information about population delimitation. But what does local mean in this context, and can scientific evidence answer the question: "How local is local?" In other words, do stands of mahogany show local adaptation, and, if so, over what geographic scale does this occur? How much similarity is there between different forests, and are neighbouring stands more similar than distant ones?

The paradigm of local adaptation is widely invoked in habitat restoration and more general seed sourcing for planting. Local genotypes are assumed to be better adapted to local conditions because natural selection increases the frequency of genes for fitness. The scale over which species show adaptation to their environment depends on the variability of the habitat characteristics that affect them (Broadhurst et al. 2008). Local adaptation, which is widespread in herbaceous plants, is not an inevitable outcome for trees. Key differences between herbaceous plants and trees suggest that many widespread trees may fail to show local adaptation at a narrow geographic scale because it may be hindered by extensive pollen/seed dispersal and opposed by selection due to environmental variation over time (Hampe and Petit 2006). Long life spans mean a site no longer necessarily experiences the same environment under which the trees originally evolved. Yearly variations in rainfall and other climatic conditions are likely to have a stabilising or balancing effect, keeping populations similar, rather than the directional selection that drives divergence among populations and can lead to highly localised adaptation.

There are two main sources of information on the patterns of genetic variation and levels of adaptation in trees. Firstly, field experiments, mainly in the form of provenance and progeny trials, can provide estimates of levels and distribution of quantitative genetic variation, heritability of particular traits, and the extent of genotype x environment interaction. Secondly, DNA-based genetic markers allow for

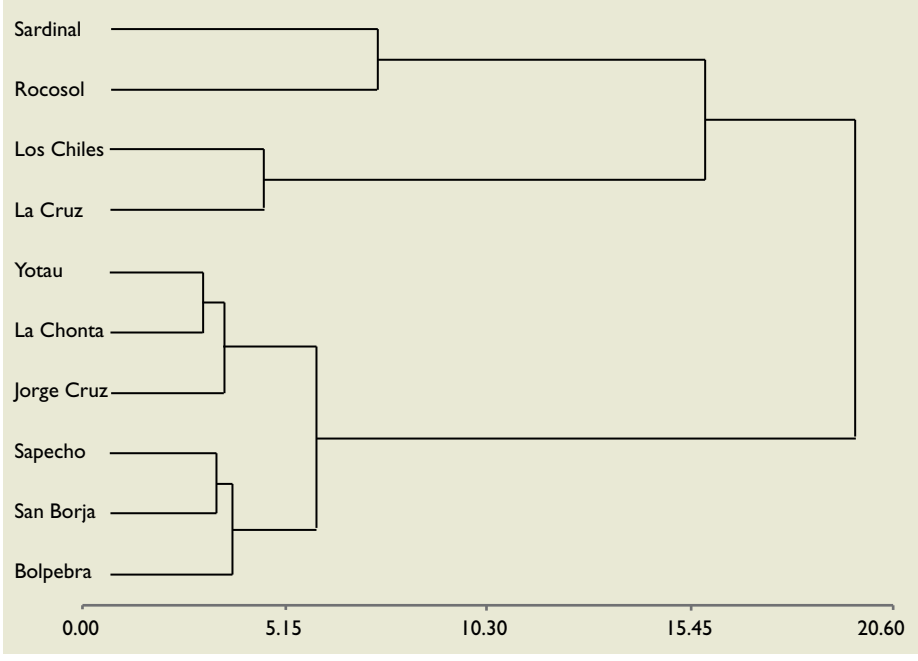

Figure 20.1 Dendrogram obtained using cluster analysis (Ward method, Euclidean distance) from populations in Costa Rica and Bolivia using the descriptors of seeds, seedlings, and dry biomass.

direct study of the distribution of genetic diversity within and between populations. Neutral genetic markers, from both nuclear and organelle genomes, can identify and potentially date (using molecular clock approaches) the occurrence of major genetic discontinuities across which there is no current gene flow (e.g., sharp climatic zones; Cavers et al. 2003, 2004; Dick and Heurtz 2008). Identification of genetically based population/adaptive differentiation has the potential to significantly influence germplasm conservation, collection, and utilisation strategies (e.g., Lowe et al. 2000, Petit et al. 2002). Molecular studies can play important roles in targeting priority areas for conservation and in determining effects of logging on genetic diversity.

20.2.1 Field Trials

The differing topography, environment, and geological history encountered across the range of widespread species can have a significant impact on genetic differentiation between regions. Across their wide geographic distributions, mahogany species appear to be adapted to a wide range of different environments and soils, e.g., heavy clay soils, seasonally flooded vertisols in flat lands, inceptisols in slopes of over 70%, rich volcanic soils, calcareous soils in dry areas, and poor soils with high aluminium or iron content (Navarro et al 2003). Trials established under a range of sub-tropical climates in Puerto Rico show clear adaptive differences between the three species with distinct responses to different climates and soils. *Swietenia macrophylla* grew best in the sub-tropical moist and wet zones, but died earliest in the dry zone. *S. humilis* grew best and survived longest in the dry and moist zones, and grew least and died soonest in the lower montane wet zone. *S. mahagoni* lived longest in the dry zone (Ward and Lugo 2003).

Existing field trials of a range of provenances (i.e., Mexico to Panama)(Figure 20.2) and species established in Costa Rica (Navarro and Hernandez. 2004), Honduras (Boshier and Billingham 2000), Mexico (Wightman et al. 2008), Puerto Rico and the US Virgin Islands (Ward and Lugo 2003) can give important information about the geographic scale of adaptive variation in *S. macrophylla*, *S. humilis* and, to a lesser extent, *S. mahogani*. In these trials, local material was tested against material collected from sites increasingly distant from the provenance trial site. For *S. macrophylla*, differences in provenances from across the Mesoamerican region show a correlation between a range of growth and survival measures (e.g., percent of germination of directly sown seed, survival and growth of 2–14 year old trees) and patterns of ecological or geographic variation (Geary et al. 1973, Newton et al. 1999, Ward and Lugo 2003, Navarro and Hernández 2004). However, this was not always reflected in local adaptation. Instead, some provenances grew well on all sites, whereas others were uniformly poor, even when grown in the climate they originated from. At the scale of provenance sampling, covering distances up to 250–450 km, no

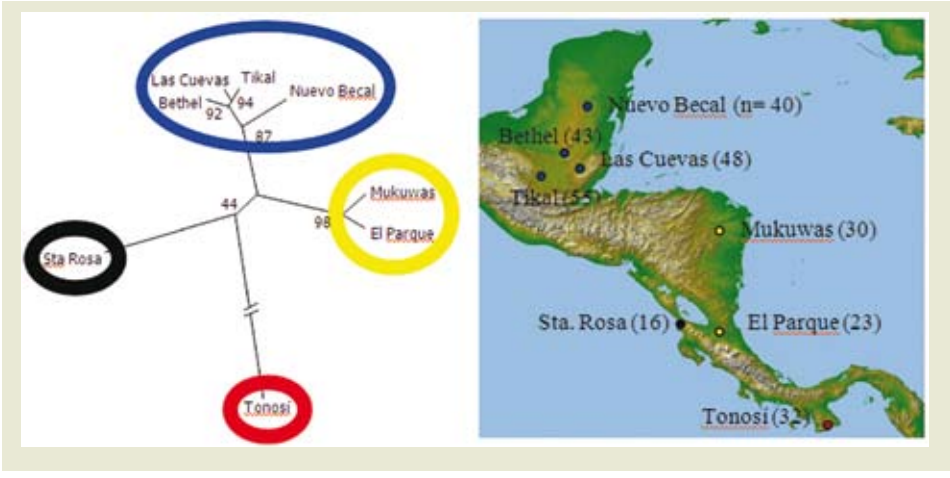

Figure 20.2 A dendrogram based on Nei's genetic distance algorithm, derived from variation at eight nuclear microsatellite loci demonstrating clustering of Central American mahogany populations based on genetic similarity (sample locations shown on map, modified from Novick et al. 2003. A similar pattern was also found by Gillies et al. 1999). Reprinted with the permission of Wiley-Blackwell.

differences were observed in terms of germination or survival. However, there was some evidence that local provenances performed better than non-local sources in terms of shoot borer *Hypsipyla grandella* attack, although this did not translate into superior growth of the local provenances. Within the Yucatan Peninsula, there were no discernible provenance differences for *S. macrophylla*, which probably reflects the shallow environmental gradients for temperature and soil in this region. Population differentiation might also be inhibited by large-scale historical disturbances from hurricanes, or deforestation due to slash-and-burn agriculture associated with historically high human (Mayan) population densities. In *S. humilis*, there were reciprocal differences between provenances, with home-site advantage for growth and survival over a 250 km distance (Honduras and Costa Rica material, Boshier 2000).

Thus, from these trials, there is little evidence for local adaptation in *S. macrophylla* and *S. humilis* at distances of less than 250 km. However, where populations are sampled across strong bioclimatic gradients, evidence for local scale adaptation exists. For example, Basil (2007) found high quantitative differentiation, as evidenced by Q_{st} values, between populations across the Guanacaste Cordillera, which separates humid and dry populations. In addition, Basil (2007) found high differentiation values between the same populations, potentially caused by the altitudinal barrier or by phenological isolation because the timing of flowering is triggered by seasonal changes, the timing of which differs on either side of the mountains. There was also a very high differentiation between populations in Bolivia and Costa Rica, which probably reflects divergent adaptation to tropical and subtropical conditions (Figure 20.1).

20.2.2 Management Units – Nuclear Variation

Nuclear microsatellite markers have been used to assess overall levels of genetic variation in mahogany populations, the differences within stands and between stands, and how this variation is distributed across Central America and Mexico. Nuclear markers reveal recent levels of pollen and seed movement between stands, i.e., the gene flow. If stands are genetically similar, there must be high levels of gene flow between them, mainly due to pollen movement. Conversely, stands with very different genetic compositions must have low levels of gene flow, resulting in little genetic mixing between them. Recent surveys of genetic variation within the mahogany nuclear genome have revealed further genetic substructuring across Central America (Figure 20.2).

Based on molecular markers (microsatellites and Random Amplified Polymorphic DNAs [RAPDs]), populations from the Yucatan Peninsula (Mexico and Guatemala) were genetically distinct from other Central American populations. Within Honduras, Nicaragua, and Costa Rica, Pacific watershed populations were distinguished from those of the Atlantic watershed (Figure 20.2). Considering that Central American countries and Mexico have several cordilleras higher in altitude than the distribution of the mahogany, they make impassable barriers that prevent gene flow, so the variation is partitioned across geographic barriers, such as mountains, as well as distance. Re-analysis of the mahogany microsatellite data from Mesoamerica in Novick et al. (2003) showed that this differentiation was better explained by an "isolation by resistance model" (McRae and Beier 2007). Within Central America, the minimum distance over which a genetic difference is observed

is about 500 km, although genetic differences between Pacific and Atlantic populations occur over shorter spatial scales (1–200 km), where climatic and physical (including soil) differences are significant. RAPDs showed that populations in Mexico had low levels of diversity, whereas a severely threatened unlogged forest fragment (Quintin, Panama) was one of the most diverse (Gillies et al. 1999). For management purposes, gene flow discontinuities should be recognised so that a "genetic unit" would comprise populations among which gene flow is significant, which, ideally, is done using molecular markers. Given conservation of a range of populations within a genetic unit (200–500 km in the case of mahogany), such a strategy would ensure a broad-based pool of standing genetic variation with potential for dispersal among populations.

20.2.3 What is the Scale of a Coherent Genetic Unit?

Analyses of spatial genetic structure and gene flow within populations indicate limited seed dispersal distances (up to 100 m, Lowe et al 2003), but much higher pollen flow distances, 200 m to 2 km in intact forest, and up to 4.5 km in fragmented areas (White et al. 2002). However, in the forest studies, the rare long-distance dispersal component was not estimated and so these maximum values are very likely to be lower limits of pollen flow; the estimates from fragmented forests show what is achievable. Analyses of regional genetic structure from both Central and South America indicate significant genetic differentiation over distances greater than 100 km (Lemes et al. 2003, Novick et al. 2003). However, in southern Amazonian populations, similar levels of differentiation were recorded only at much greater geographic distances (up to 500 km) (Lemes et al. 2003). The differences between these two ranges is likely to be due to the increasing topographic and environmental variability in Central America, compared to the relatively homogenous, flat landscape across the southern Amazon basin (Lemes et al. in press). Considering these parameters, a coherent genetic unit, or population, is likely to be comprised of individuals within 10–50 km of each other. This estimate depends on intervening habitat and landscape, since it is likely to be lower in a topographically or environmentally variable area, and higher across homogenous or partially fragmented landscapes (unless fragmentation presents a barrier to gene flow). It should be noted that this estimate of population size indicates a coherent genetic unit, i.e., the spatial distance over which genes are likely to be exchanged over generations. Such a unit should be used for defining the scale at which provenances or populations can be sampled for collection or study. Due to the low genotype by environment interaction within regional areas for *S. macrophylla* (Navarro and Hernandez 2004), these estimates should not be used to restrict the movement of provenance material for restoration, since such material can be transferred over distances up to 500 km.

20.3 Good Seed Collection Practice

Poor seed collection practice leads to establishment of trees with restricted genetic diversity. Limited seed collection will constrain genetic makeup and may result in lack of genetic variation that can respond to local conditions, whatever the provenance of the seed. Collected seed needs to have a broad genetic base in order to prevent inbreeding depression and ensure that planted stands remain viable, producing seed in the short term and maintaining the ability to adapt to changing environments. To maximise genetic diversity in seed collections, it is necessary to collect from as many seed trees as possible; the minimum number of trees depends on the species and the purpose of the collection. However, decisions often need to be made about which stands to collect from; which trees within the stands; whether to collect from isolated trees; and whether to collect in poor seed years. Studying the reproductive biology of a species can tell us about the amount and pattern of distribution of genetic variation and also about the factors that determine this distribution.

20.3.1 Selfing and Mating Patterns

Close inspection of *Swietenia humilis* flowers (Figure 20.3) reveals that individual flowers are either male or female, both are found on the same tree, and that all three species are monoecious. Detailed studies in *S. humilis* and *S. macrophylla* show that the ability of any tree to produce fruit varies from year to year (Boshier et al. 2004, Grogan and Galvao 2006). In *S. humilis*, this is owing to yearly variation in the production of female flowers (White and Boshier 2002, Boshier unpublished data). Thus, in a given year, a tree may flower but may not produce fruit owing to little or no production of female flowers. As such, the extent of flowering is not a good predictor of seed production. This concurs with local informants' views for both *S. humilis* and S. *macrophylla*, that trees are high seed-producers in some years and not in others; however, the broader extension of this observation to other species in this genus is unknown. The flowers show no structures

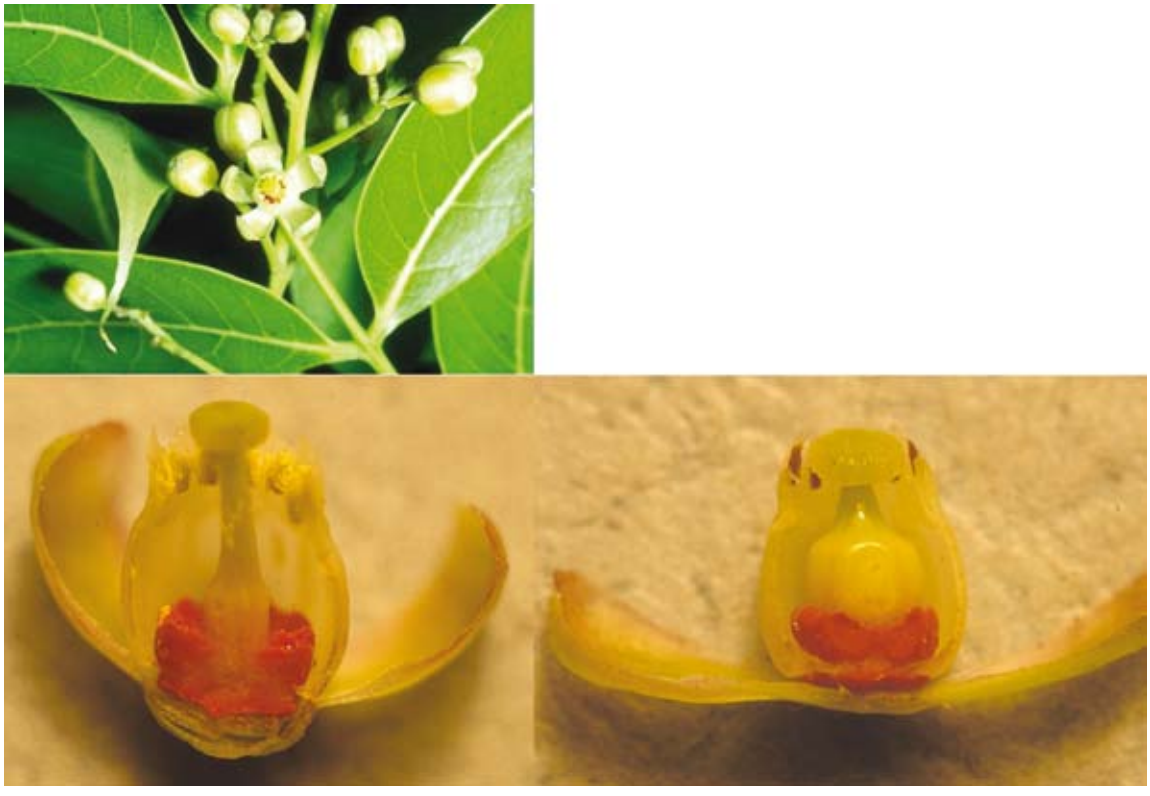

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Figure 20.3 Floral whorl (top), and male (left) and female (right) flowers of *Swietenia humilis*.

with apparent specialisation for specific pollinators, and produce small quantities of nectar such that they are attractive to a wide range of insects (Boshier unpublished data). The extent of pollination is thus unlikely to be affected by habitat disturbance that can reduce the occurrence of particular specialist pollinators for other species.

In any single tree, the production of female flowers is restricted to a much shorter period (mean = 11.5 days) compared to male flowers (mean = 32 days). Individual trees are therefore receptive to pollen for a much shorter period than they can disperse pollen and so generate seed. The short female flowering period reduces considerably the number of potential pollen sources open to any one tree (White and Boshier 2000). Asynchrony of flowering between individual trees in a population may also limit the number of pollen sources, resulting in a reduced number of potential trees to generate seed on any particular tree. Thus, neighbouring trees may not cross-fertilise, or effective pollen flow (pollen that produces seed) may be unidirectional; this may be another factor influencing variable fruit set. Both molecular markers and controlled pollinations also demonstrate that *S. humilis* is highly self-incompatible. Of 17 trees studied, only one showed any level of selfing (White and Boshier 2002), while of more than 45 attempted selfs carried out on 12 trees, not one capsule was produced, showing a strong level of self-incompatibility (Billingham 1999).

20.3.2 How Many Capsules to Collect From a Tree?

Female flowers have large numbers of ovules, such that one capsule may contain >60 seeds. However, molecular studies in *S. humilis* show that the number and source of pollen donors varies between capsules and trees (White et al. 2002). Thus, the seed from one capsule may share both male and female gametes (i.e., be full sibs) or only a few common pollen donors may account for most of the fertility across all potential males. Collection from a number of capsules ensures a diversity of pollen sources and consequently helps to maintain genetic diversity, but this also should go together with the collection from several parent (female) trees, which is highly advised.

20.3.3 How Many Trees to Collect From?

This question is often raised by seed collectors. There is no single correct answer since it depends both on the aim of the collection and the way in which genetic diversity is distributed within the stand. It is not possible to sample all the diversity present in a population unless the whole population is collected,

and this is clearly impractical. So while, ideally, one might look for "conservation of as much of a population's genetic diversity as possible," in terms of sample size, there are diminishing returns. As the number of seed trees sampled increases, the amount of extra diversity collected is reduced. In outcrossing *Swietenia* species, when fruits/seeds are collected (assuming collection of at least 500 viable seeds per tree, equivalent to 15–25 fruits per tree), adequate sampling depends on the number of seeds collected per tree and the mating/pollination system of the tree species. Since insect pollination can lead to only a few fathers siring seed for individual trees, the number of trees to sample from should be maximised. Seed from 15 trees will contain an arbitrary target of 95% of alleles with a frequency of >5%, while a collection from 30 trees will include additional rare alleles (95% of alleles with a frequency of >2.5%); only a slight increase in the genetic diversity (based on general modelling results from a range of tropical tree species) (Kremer et al 2005). The problem is that in some cases community foresters sometimes only collect from one or two trees, while seed banks often target less than 10 trees for a bulk collection. Adherence to these guidelines would ensure higher levels of diversity are collected than would result from most current seed collection practices.

20.3.4 What Should Be the Spatial Separation between Sample Trees?

In addition to considering the number of seed trees, collection guidelines should also specify the spatial separation between target trees. Within natural populations of many species, spatial genetic structure is generated by the processes of pollen and seed dispersal. If a high proportion of seeds fall close to the female tree, this can produce a group of genetically related individuals (siblings or half siblings). Collecting from such a group may reduce the genetic diversity within restoration plantings or, if this material is then allowed to reproduce, may cause inbreeding depression by forcing between closely related "family members" (termed biparental inbreeding in botanical situations). To avoid making seed collections from closely related individuals, it is prudent to specify a spatial separation between trees over which spatial genetic structure is likely not to be an issue. While collection from trees at distances greater than mean seed dispersal distances should avoid genetically related "maternal" parents, collection from trees at this minimum distance will essentially sample the same local pollen pool. Clearly, if a collection is to be as representative of a population's gene pool as possible, and sample a maximum of its genetic diversity, it must take account of the fact that seed dispersal is generally more limited than pollen flow and be guided by the latter (Levin and Kerster 1974).

Several types of data can be used to provide appropriate guidelines for spatial sampling to maximise genetic diversity. Within Amazonian forest populations, while most S. macrophylla seed falls out within the first 30-50 m, dispersal distances of up to 80 m have been recorded (Gullison et al. 1996, Grogan and Galvão 2006), and there is evidence that in open or cleared habitats, seed dispersal may be even greater (up to 300 m for S. humilis) (White and Boshier 2000). Even longer pollen dispersal distances have been recorded for mahogany species. Using genetic assignment methods, it was found that 40–60% of pollen dispersal distances were less than 300 m for *S. humilis* inhabiting both intact and fragmented remnant forests (White and Boshier 2000). However, within forest fragments, 20–50% of pollen was dispersed in excess of 1 km and, for an isolated tree, a dispersal distance of over 4.5 km was recorded for nearly 40% of pollinations. Therefore, to avoid sampling half-sib or closely related individuals that occur in clusters, it is advisable for seed collections to leave >200 m between trees targeted for seed sourcing.

20.3.5 Can We Collect from Isolated Trees?

For sourcing seed, isolated trees within pasture or agricultural contexts represent ideal targets since they are easy to identify and access. Also, removal of surrounding vegetation and, in some cases, supplemental fertilisation from surrounding crops leads to profuse flowering and fruiting. However, do these types of seed sources represent healthy genetic populations?

A large growth trial was carried out with the purpose of assessing if seed from isolated trees produced seedlings that were less vigorous than those from forest populations for *S. macrophylla*. Seeds were sourced from trees in different habitat contexts classed as: isolated (>500 m to nearest conspecific), semi-isolated (1 conspecific within 500 m), clustered (conspecifics within 100 m of seed tree), from across Central America (Yucatan to Panama), and grown in common garden conditions in Costa Rica (Navarro et al. 2010). For *S. macrophylla*, a single common garden trial of 30 individuals from each of 91 families (2730 seedlings) was established in Los Chiles, Alajuela, in Costa Rica. For the numbers of families and progeny in each ecogeographic source region and female tree isolation context class, see Table 20.1. For seeds from trees in the isolated context, there was a significant reduction in seedling/tree growth compared to seeds from the other contexts (semi-isolated and clustered), which were very

Table 20.1 Number of female trees and progeny (in parentheses) evaluated for each region and isolation class in *Swietenia macrophylla*.

S. macrophylla	Yucatan Peninsula, including NE Guatemala	Atlantic Coast of Honduras and Nicaragua, and northern Costa Rica	Pacific Coast of Costa Rica and Panama
Isolated	7 (210)	16 (482)	17 (506)
Semi-isolated	4 (120)	4 (120)	1 (30)
Clustered	20 (600)	18 (526)	4 (106)

Table 20.2 Mating system parameters by isolation class, with standard errors in parentheses for *S. macrophylla* trial. Values obtained by analysis of genotypic data from approximately 20 seedling per female tree, and more than 30 female trees.

	Isolated	Semi-isolated	Clustered
Outcrossing rate	0.919 (0.023)	0.987 (0.001)	0.976 (0.005)
Biparental inbreeding	0.389 (0.037)	0.362 (0.010)	0.353 (0.046)
Correlation of paternity	0.452 (0.125)	0.330 (0.162)	0.220 (0.080)

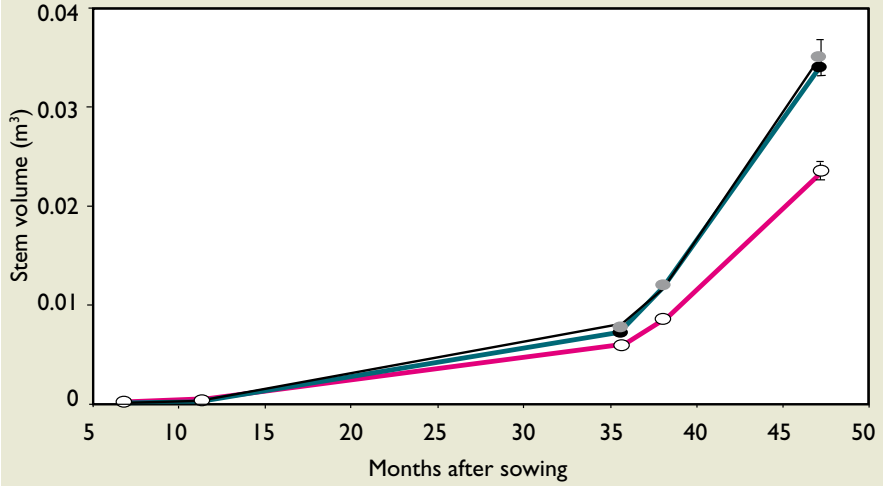

Figure 20.4 Plot of seedling/tree growth (as stem volume) over time for *Swietenia macrophylla* progeny sourced from isolated (no congeners within 500 m, white circles), semi-isolated (conspecifics present within 100–500 m, grey circles) and clustered trees (more than two conspecific trees within a radius of less than 100 m, black circles), from Navarro et al. (2010).

similar. Means and standard errors are presented in Figure 20.4.

In addition, when this material was surveyed using nuclear microsatellites to analyse mating system patterns, isolated trees showed significantly higher levels of selfing, biparental inbreeding, and lower numbers of sires, (as measured by correlation of paternity). However, the strongest correlation with the growth data was the number of fathers per seed tree. Thus, for *S. macrophylla*, trees in an isolated context are receiving pollen from a smaller number of trees (i.e., higher correlation of paternity, see Table 20.2), which negatively impacts on the performance of their progeny. Again, semi-isolated and clustered trees showed similar trends to one another. In this study, and in another looking at the mating system of *S. macrophylla* from Brazil (Lemes et al. 2007), true selfing was only exhibited by a relatively low number of trees (<15%). For the Central American study, when these individuals were removed, the effects of biparental inbreeding and number of sires on fitness remained. However, when this aspect was investigated for *S. humilis*, although isolated trees received lower numbers of pollen donors (White et al. 2000), there was no difference in the growth of progeny from different contexts (Boshier and Billingham 1999).

20.4 Lessons for Managing Natural Forests and Landscape Contexts

20.4.1 Sustainable Logging: How Many Seed Trees to Leave?

Logging represents a reduction in density of reproductively mature trees in a population. Obviously, the extent of the reduction will depend on the intensity of logging, which varies from country to country and whether it is legal or illegal. For example, in Brazil, the minimum legal cutting diameter is currently 60 cm dbh (diameter at breast height) with retention during the first harvest of 20% of commercial-sized trees and a minimum retention density of 5 commercial-sized trees per 100 ha. In Belize, loggers, generally operating illegally, high-grade most (>95%) trees of commercial size, down to 20 cm dbh in some regions (Weaver and Sabido 1997).

Simulation studies (e.g., Lowe et al. 2005) indicate that, depending on the extent of flowering densities and decreased population size, logging can lead to loss of genetic diversity in several generations. For example, with a remnant population of 20 reproductively mature individuals, 10% of allelic variation is lost in two generations, and 20% in three generations; whereas, for a remnant population of 50 individuals, 5% of the allelic variation is lost in four generations, and 10% in seven generations. Severe reductions can be expressed in a single generation in heavily logged areas (Lowe et al. 2005). In theory, a minimum of 500 individuals is required to sustain genetic diversity within a population (Franklin 1980, Soule 1980). However, due to temporal variance in effective population size, more like 1000 reproductively mature trees need to be retained within a reproductively coherent unit (a scale of approx 5–50 km) to maintain genetic diversity (Degen et al. 2006). *Swietenia macrophylla* trees greater than 30 cm dbh are considered to be of reproductive size (Grogan 2001). From a genetic perspective, the minimum number of seed trees required per ha, therefore, depends on the pollen dispersal dynamics of the species and the size of forest where pollen flow occurs without any isolation/fragmentation. A conservative estimate, taking 1.5 km as the limit of pollen dispersal/connectivity, would equate to leaving approximately 1 seed tree per ha, following logging, assuming that 1000 ha of suitable mahogany habitat remains. For smaller blocks, the density will need to be higher. Thus, for the 4100 ha Marajoara rainforest management area, where surrounding forests were cleared for ranching and agriculture, pre- and post-logging commercial densities (>45 cm dbh) for *S. macrophylla* were 0.51 and 0.08 trees/ha, respectively (Andre et al. 2008). These densities translate to pre- and post-logging commercial population sizes of 2091 and 328, respectively, which can explain the observed post-logging loss of genetic diversity (Andre et al. 2008). Based on *S. macrophylla* densities from eight other forest sites in the Brazilian Amazon (Grogan et al. 2008), the area of genetically connected forest required to sustain sufficiently large populations without loss of genetic diversity (>reproductive 1000 trees) is large, varying from approximately 1500–100 000 ha, even prior to any logging.

20.4.2 Potential for Tracing Timber Source

All three species of *Swietenia* are CITES-listed, and, as timber, difficult to tell apart, macroscopically and microscopically, from other Meliaceae species that are also marketed as "mahoganies." The potential to develop a DNA tracking methodology for natural mahogany populations, which can distinguish between countries of origin, is high. Chloroplast variation can be used unambiguously to distinguish between Central and South American sources of *S. macrophylla* (Lemes et al. in press), and within these regions, nuclear markers can provide genetic resolution over a 100–500 km scale (Lowe 2008). The ability to distinguish between sources will depend on the intensity of sampling across different populations/regions. In addition, some commercial plantations have very good records indicating the regional, and in some cases, population source that was used during planting. It would be prudent to test some of these historical records using genetic markers that distinguish between putative sources. As well, verification that timber is sourced from sustainable rather than illegally logged natural populations should involve the genotyping of plantation sources and establishment of a database of plantation genetic profiles for independent consumer checking.

20.4.3 Harnessing Natural Regeneration and Directing Forest Restoration

Following forest fragmentation, mahogany can be a successful coloniser of cleared areas. In a seed dispersal study of the pioneer species *Vochysia ferruginea* (a hardwood rainforest tree) in Costa Rica, it was found that only a limited number of trees, those on the periphery of the intact forest, contributed to recolonisation of cleared areas (Davies et al. in press). This type of dynamic can lead to a significant genetic diversity bottleneck in recolonised areas that may persist for several decades. Successful recolo-

nisation will depend on the density of the species involved and the genetic diversity of the population. Over time, genetic diversity may be supplemented in these areas by pollen flow from diverse surrounding sources. However, this assumes that the recolonised area is relatively small compared to neighbouring intact forest. Alternatively, if there is a large but genetically depauperate area of recolonisation due to the initial colonisation bottleneck, then genetic diversity within the source population could be significantly reduced by "pollen swamping" (great local excesses of pollen in which few male plants fertilise nearly all of the offspring in the population), in giving great local excesses of pollen) if the source is a small and isolated remnant. Restoration of genetic diversity in recolonised areas also depends on the maintenance of genetically diverse remnant populations in the landscape. If there is a risk of such genetic bottleneck scenarios, natural regeneration should be supplemented by restoration plantings using diverse stock (see section 20.3 on good seed collection practice, and discussion below).

Activities to restore genetically diverse mahogany forests need to consider the full scope of the provenance and seed collection guidelines presented above. In terms of the source location of stock, the low genotype-by-environment interaction for *S. macrophylla*, at least within a region (Navarro and Hernandez 2004), means that in most cases germplasm can be transferred across distances of up to 500 km without major fitness implications. Some important qualifications to this statement are that a major biogeographic divide occurs between Central and South America and so it is recommended that stock remains within these continents. In addition, several important ecogeographic regions occur across the species range, including: the Yucatan Peninsula; Atlantic zone Honduras, Nicaragua and Costa Rica; Pacific zone Costa Rica/Panama; Atlantic coast Colombia and Venezuela; and the Amazon basin (Colombia, Ecuador, Peru, Bolivia, and Brazil), based on a combination of neutral genetic and provenance variations (Gillies et al. 1999; Lemes et al. 2003, 2010; Novick et al. 2003; Navarro and Hernandez 2004). Keeping provenances within these regions is recommended if the intention is to match source/target adaptation. However, in some cases, non-local sources have superior growth performance (see section 20.2.1).

In terms of seed collection practices that maximise diversity and vigour for restoration programmes, the following recommendations need to be considered:

- A coherent genetic unit (population) will have a spatial scale of 10–50 km, depending on the environment.
- Seed will need to be sampled from 15–30 trees per population to sample 95% of the population's genetic variation.
- Sample trees should be spatially separated by >200 m to minimise the chance of sampling closely related individuals.
- Several capsules per tree should be sampled, and seed from different capsules mixed.
- Very isolated trees (more than 500 m to nearest congener) in non-forested contexts (e.g., pasture) should be avoided in favour of those that have one or preferably more trees of the same species within a 500 m radius in order to improve seedling vigour.

20.4.4 Biodiversity Corridors, Landscape Mosaics, and Trees Outside Forests

Biodiversity corridors are widely used as a landscape conservation tool to increase population sizes, connect forest remnants, and allow latitudinal migration and ecotonal adaptation. Although in the majority of cases, continuous, intact, native habitat is the optimal solution for biodiversity outcomes, many remnant areas are separated by economically or socially important matrices (e.g., farmland or settlements). In such cases, alternative "corridor" strategies need to be considered, such as stepping stones and narrow linear routes (e.g., road-side verges). To establish biological corridors, there is also a need to understand how species migrate through different corridor and matrix types.

To avoid losing genetic variation and allow for future evolutionary adaptation at the population level, isolated remnant stands should contain a minimum of 1000 trees. Establishing corridors that increase connectivity, and also population size, among remnants is to be encouraged. The critical genetic resource information relevant to biodiversity corridor planning for mahogany is:

- Seed dispersal dynamics vary between forest and open contexts, where maximum distances of 80 and 300 m, respectively, are recorded.
- Pollen dispersal distances vary dramatically between forest and open contexts, where maximum distances have been recorded as 200 m and 4.5 km, respectively. Rare long distance dispersal may occur over even greater distances.
- To ensure that forest patches can form a stepping-stone corridor, a distance of not more than 5 km will allow connectivity between mahogany populations. The ability to link larger reserve areas containing more than 1000 individuals and provide sources of evolutionary adaptation through a series of stepping stones, probably offers the best compromise to maintain species-level diversity.

This will offer migration pathways for climate change, maximise evolutionary potential, and minimise land-use area for conservation and allow intermixing with other social and economic land uses.

- Mahogany is a light-demanding, long-lived species that colonises gaps in undisturbed forest and that can rapidly colonise open areas. If previously cleared areas (e.g., pastures) are abandoned close to a mahogany remnant (within 200 m), mahogany will be able to establish and compete with other natural regeneration. Therefore, the natural ability of mahogany to recolonise abandoned farmland can be harnessed over short distances; for locations more distant from a mahogany-containing remnant (>200m), supplemental planting is recommended.

Corridors and stepping-stone populations in the landscape may also contribute to other aspects of genetic resource management and conservation for mahogany, for example:

- Conservation of particular genotypes not found in reserves;
- Facilitation of gene flow between existing reserves;
- Maintenance of minimum viable populations; and
- Intermediaries and alternate hosts for pollinators.

20.5 Conclusions

This chapter draws attention to ongoing high reductions in the populations of this economically important species due to a range of threats. To combat further decline, effective conservation and management programmes are essential. The previous sections show how genetic information can be used to help define the practical details that are needed if conservation and management programmes are to be successfully implemented. There are, however, some problems associated with efforts to conserve exploited but endangered species like mahogany. Considering *Swietenia* spp.'s (particularly *S. macrophylla*) wide distribution (geographic, ecological, socio-political), conservation and sustainable management of it's the genus' genetic resources cannot be simply defined in terms of one-size-fits-all solutions. Completely protected areas (e.g., Tikal National Park) can protect mahogany effectively mainly because additional resources (e.g., from archaeological tourism) provide adequate park protection. However, other areas of natural forest that have protected status are extraction reserves (e.g., the Maya Biosphere Reserve), where *S. macrophylla* is exploited and potentially not adequately conserved. Indeed, in some reserves, mahogany is the only species exploited, which reduces its ability to compete with other highly prolific and aggressive pioneer species and makes it rare or totally absent in areas close to roads. The conservation and sustainable use of mahogany and other high value and endangered species requires involvement of the local communities, as well as higher level political support, to prevent illegal logging and ensure mutual benefits.

Forest management can play an important role in regenerating this species, which is light-demanding and has higher fruit production in open conditions (Mayhew and Newton 1998, Boshier et al. 2004, Grogan et al. 2005). However, the type of management applied must take into account both the successional stage and ecological zone of the forest (Brown et al. 2003). While *S. macrophylla* can regenerate after catastrophic disturbance (e.g., hurricanes that open the forests and give seed trees the space to deliver seeds) (Snook 1996), it is not necessary for the species persistence in semi-deciduous forest, where much greater penetration of light permits dense recruitment. Brown et al. (2003) argue that in late-succession wet forest, *S. macrophylla* typically occurs at low densities, persisting as relict populations in the process of competitive exclusion. There are few seedlings and saplings, and only rarely do they survive and grow to form advance regeneration. Options to generate long-term sustainably harvested stands of *S. macrophylla* are limited to artificial regeneration, either through direct seeding (Negreros-Castillo and Hall 1996) or planting seedlings (d'Oliveira 2000). In drier forests and those at earlier successional stages, population densities of mahogany tend to be higher with more juveniles relative to adults, and more prolific advanced regeneration (Stevenson 1927, Baima 2001). Here, reduced impact logging will be sufficient to stimulate natural regeneration of *S. macrophylla*, which should benefit from small-scale disturbance (Brown et al. 2003).

In addition to *in situ* conservation, it is important to recognise that for *Swietenia* spp., large numbers of trees and populations exist outside of forests (often in pasture contexts), and there is an urgent need to develop efforts at the landscape level for their effective management. There is also a need to raise awareness among development professionals of the value of natural regeneration as both a conservation and socio-economic resource. Promotion of a limited range of species, often exotics, by development agencies, may reduce the potential genetic benefits of such systems, in addition to creating potential problems of invasiveness. However, there is also a need for conservation planners who are more accustomed to using *in situ* methods to consider the possibility that populations of trees found outside protected areas have a role in the conservation of biodiversity.

This requires the direct involvement of development organisations in biodiversity conservation and effective two-way communication with "traditional" conservation organisations to ensure both conservation and development benefits.

In conserving a species with a wide geographic range like *S. macrophylla*, promoting collaboration between countries for collecting, characterising, and conserving genetic resources is vital. Evidence of the benefits is seen in the seed collection efforts required to comprehensively assess the scale and use of adaptive genetic variation. In Mesoamerica, where *S. macrophylla* has experienced severe impacts, a consortium of research organisations – World Agroforestry Centre (ICRAF) and National Institute for Agricultural, Livestock and Forestry Research of Mexico (INIFAP); Forest Department, Las Cuevas Experimental Station, Rio Bravo Conservation Area in Belize; National Council of Protected Areas (CONAP) National Park Tikal and Centro Maya in Guatemala; Escuela Nacional de Ciencias Forestales (ESNACIFOR) and Proyecto Desarollo del Bosque Latifoliado (PDBL) in Honduras; Centre for Genetic Improvement and Forest Seeds in Nicaragua; Asociacion Nacional para la Conservacion de la Naturaleza (ANCON) and Instituto Nacional de Recursos Naturales Renovables (INRENARE) in Panama – participated in the collection and evaluation of mahogany populations. The collections made are the most extensive across the distribution of *S. macrophylla*, with a large part of them made outside of protected areas (Navarro et al. 2003). Nevertheless, such collaboration between researchers at universities and research centres becomes increasingly problematic under new procedures associated with the Convention on Biological Diversity (CBD). New laws that regulate the exchange of material with the intention of preventing biopiracy and recognising country and local communities' rights/ownership have made it more time-consuming and difficult to obtain and exchange seeds/leaves among researchers within those same countries. A consensus between countries at regional and international levels is recommended – because phytosanitary rules are different from country to country – to facilitate the exchange of forest reproductive material and assist genetic resource conservation efforts.

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